Temporal and spatial patterns of abundance in the gastropod assemblage of a macrophyte bed

Kenneth M. Brown

Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana U. S. A. 70803, zobrow@lsuvm.sncc.lsu.edu

Abstract: Although gastropods are more common and diverse in macrophyte beds than in areas without littoral vegetation, little is known of fine-scale patterns of abundance within macrophyte beds, or changes in abundance of species through time. I present data here on such patterns in the gastropod assemblage found in Carrol Lake, Wisconsin. The assemblage was quite diverse, with 13 species, four of which had mean densities greater than 100/m^2. The assemblage was dominated by small, thick-shelled species, especially *Amnicola limosa* Say, 1817. Gastropod density decreased across two field seasons, although trends within each field season were for increases with time in the abundance of most species, especially in shallower habitats. At the micro-habitat scale, abundances of the most common species were positively correlated, perhaps because they prefer to colonize the same macrophytes, based on the results of laboratory macrophyte-choice experiments.

Key words: gastropods, micro-distributions, macrophyte choice

Gastropods are clearly more abundant and diverse in macrophyte beds than in littoral-zone habitats without vegetative cover (Brown *et al.*, 1988; Brown, 1991; Brown and Lodge, 1993). However, few studies have considered fine-scale patterns in the abundance of gastropod assemblages within macrophyte beds, or how such patterns vary through time or space. In an earlier paper (Brown and Lodge, 1993), we studied whether gastropod distributions at the macrohabitat (*e. g.* sand versus cobble versus macrophytes) scale were determined by habitat choice. Specifically, we worked experimentally with several gastropod species common in northern Wisconsin lakes, and found that most species, on a surface-area specific basis, preferred cobble over macrophyte substrata. However, given the fact that total abundances and diversity of gastropods are still greater in macrophyte beds because of the greater substratum surface area per unit bottom area, I consider it still important to look at patterns of microdistribution and habitat choice within macrophyte beds.

Here I present such data describing temporal and depth-related trends in the abundance of a gastropod assemblage in a macrophyte bed in a northern Wisconsin lake. I present data on changes in the abundances of gastropods over two seasons, and describe how abundances change through time within each season at different depths. I am also interested in whether gastropods show similar use of space at the micro-habitat (*e. g.* single sample) level. Finally, I test for differences in macrophyte choice, with several gastropod species, on several macrophytes common in northern Wisconsin lakes. The purpose of these experiments was to determine if the high levels of overlap of species at the micro-habitat level (see results) could be explained by similar patterns of macrophyte use.

METHODS

SAMPLING OF GASTROPODS

Sampling was conducted in the near-shore littoral zone of Carrol Lake, a circum-neutral, mesotrophic lake in Vilas County, Wisconsin (for a general description of these lacustrine habitats, see Lodge *et al.*, 1994). Temperatures ranged from 2-3°C in winter to a maximum of 20°C in late summer. Dissolved oxygen readings ranged from 10 mg/l in summer to 5 mg/l in mid-winter, underneath the ice. Substrata changed from sand and cobble in the first few meters from shore to sparse macrophytes, and then a dense macrophyte bed at depths greater than 0.5 m (Fig. 1). Filamentous green algae were common on the cobble and sand, and macrophyte diversity increased with distance from the shoreline. The most common macrophyte species were *Vallisneria americana* Michaux, *Elodea canadensis* Michaux, *Potamogeton robinsii* Oakes, *Sagittaria* spp., *Najas flexilis* Rostkovias and Schmidt, *Ceratophyllum*

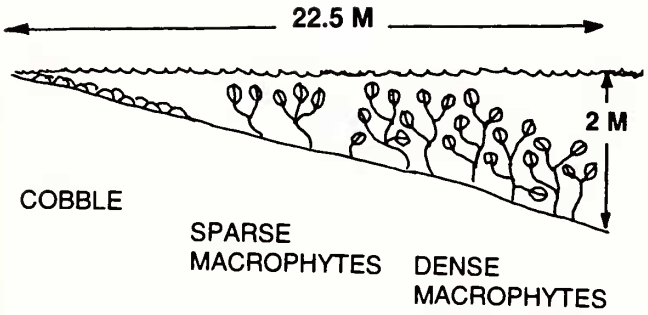

Fig. 1. Transect of the sampling site, indicating depth, substratum type, and macrophyte density.

demersum Sieber ex Chamisso, *Megalodonta beckii* Greene, *Myriophyllum exalbescens* Fernald, *P. amplifolius* Tuckerman, and *P. richardsonii* Rydberg.

A 500 m^2 section of littoral zone (approximately 22.5 m along the shoreline and 22.5 m out into the lake) was marked off along the northeastern shoreline of Carrol Lake, and all sampling was conducted within this area. The site was sampled over two field seasons in 1990 and 1991. In each season, five sampling groups were completed. The first sampling group was within two weeks of ice-out (usually in mid-May), and each successive sampling group was taken at approximate three-week intervals through the summer, with final sampling in late September. Each sampling group consisted of eight benthic cores, stratified into three depth bands based on relative area within the 500 m^2 area: inshore (less than 0.5 m depth, two samples), mid-depth (0.5-1 m depth, three samples), and deep (greater than 1 m depth, three samples). The 500 m^2 area was divided into 3 x 3 m plots, and these 9 m^2 plots were chosen randomly within each stratum at each date for sampling.

A 0.3 m-long benthic corer, constructed of 15 cm-diameter PVC pipe (sampling area = 182 cm^2), was inserted by two SCUBA divers 3 cm into the substratum so that a horizontal slit in the side of the corer was at least 1 cm below the sediment surface, and an aluminum restraining plate was inserted. The top 1 cm of sediment, overlaying macrophytes, and any snails in the sediments or macrophytes were then collected in the corer. A large plastic bag was held over the corer as it was brought to the surface to ensure that macrophytes or gastropods were not lost from the sample. More details on the corer and basic sampling methods can be found in Klosiewski (1991) and Lodge *et al.* (1994) .

Samples were processed through a series of sieves (ranging from 2 mm to 0.5 mm mesh) to remove fine sediments but retain snails, which all have a minimum diameter greater than 0.5 mm (Lodge *et al.*, 1987, 1994). Samples were then sorted in shallow enamel trays with the aid of a magnifying lens and light (Brown, 1991). Macrophytes were removed and vigorously shaken in a water-filled tub to dislodge gastropods (preliminary experiments revealed this technique increased snail recovery and minimized time spent sorting).

Gastropod abundances were converted to a per m^2 basis, and both total gastropod abundance and the abundances of the each of the five most common gastropods were analyzed in a three-way analysis of variance (two years times five sampling groups times three depth strata). I considered year, sampling group, and depth to be fixed effects. Abundances were log-transformed before analysis of variance because of mean-variance correlations, but raw data are portrayed in all figures. Thus, I could look for seasonal, yearly, or depth-related trends in the abundance of the whole gastropod assemblage, along with differences among the distributions of each of the five most common species.

To assess more fine-grained differences in the distributions of the gastropods, I also looked for correlations in the abundance of the snails on a per sample basis. This is essentially equivalent to calculating niche-overlap values for each of the species pairs, because most niche-overlap metrics (for example, the traditional Levins-MacArthur overlap statistic) are similar to correlation coefficients (Brown, 1982). The Pearson product-moment correlations were calculated from data pooled over both years, all sampling groups, and depths.

MACROPHYTE COLONIZATION EXPERIMENT

This experiment was conducted indoors at the Trout Lake Biological Station of the University of Wisconsin in July 1987. The experimental units were circular plastic tubs, 50 cm in diameter and 15 cm deep, with a sand substratum of 2 cm and a water depth of 12 cm. Water temperature was 20°C and lighting was on a 14L:10D schedule. Each pan had six stems each of four macrophytes: *Ceratophyllum demersum, Elodea canadensis, Potamogeton robinsii*, and *P. richardsonii.*

These macrophyte species were chosen both because they are common species in northern Wisconsin lakes (Lodge *et al.*, 1994), and because they vary in morphology, ranging from thin-leaved (*Ceratophyllum* and *Elodea*) to relatively broad-leaved (both *Potamogeton* spp.). The wet masses of the individual stems were chosen so that surface area was standardized among the four species at 64 cm^2. These masses were 0.71 g (*Elodea*), 1.2 g (*Ceratophyllum*), 0.85 g (*P. robinsii*), and 0.93 g (*P. richardsonii*). Standardization of surface area was necessary because colonization rates are dependent on surface area (Kershner and Lodge, 1990). Stems were hap-hazardly inserted in the sand substratum, and weighed down with lead strips so that stems were vertical.

Fifty snails of each of four gastropod species were

introduced in mono-specific populations to the tubs. Numbers of snails colonizing each macrophyte were recorded after 8 hr because preliminary experiments indicated colonization peaked by that interval. Four species were chosen either because they were abundant in Carrol Lake (*Amnicola limosa*, Say 1817; *Physa gyrina* Say, 1821; *Helisoma anceps* Menke, 1830), or to represent the range of pulmonate families common in these Wisconsin lakes (*Lymnaea emarginata* Say, 1821). There were five replicates for each gastropod species. Statistical analysis of the data was as a two-way analysis of variance (four snail species times four macrophyte species), with a split-plot arrangement of treatments (macrophyte species were present as sub-plot variables in tubs with each gastropod species).

RESULTS

GASTROPOD SAMPLING

The gastropod assemblage of Carrol Lake was quite diverse and abundant (Fig. 2), with 13 species total. Four species had mean abundances (over all sampling groups in both years) greater than 100 individuals per m^2: *Amnicola limosa* (a caenogastropod), *Valvata tricarinata* (Say, 1817) (a "lower heterobranch"), and *Gyraulus parvus* (Say, 1817) and *Physa gyrina* (both pulmonates). Four additional pulmonates had intermediate levels of abundance (greater than 5/m^2): *Helisoma anceps*, *H. companulatum* (Say, 1821), *G. hirsutis* (Say, 1817), and *Promenetus exacuous* (Say, 1821), along with the caenogastropod *Campeloma decisum* (Say, 1816). Four additional species were rare (*e. g.* collected in fewer than five of the sampling groups): three pulmonates [*Helisoma trivolvis* (Say, 1817), *Fossaria galbana* (Say, 1825), and *Laevapex fuscus* (Adams, 1841)], and one caenogastropod [*Viviparus georgianus* (Lea, 1834)]. Most of the common gastropods were fairly small (Fig. 2), with the six most common species averaging (again over all sampling groups) less than 10 mm in shell length (spiral-shelled species) or diameter (plano-spiral species).

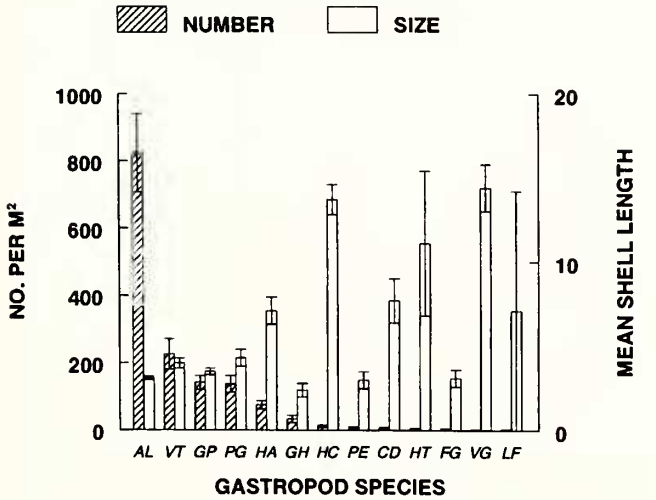

Fig. 2. Abundance of gastropod species, averaged over all sampling groups, years, and depth strata, ± standard errors, along with mean shell lengths ± standard errors. See Table 1 for the acronyms of the five most common species. (CD, *Campeloma decisum*; FG, *Fossaria galbana*; GH, *Gyraulus hirsutis*; HC, *Helisoma companulatum*; HT, *H. trivolvis*; LF, *Laevapex fuscus*; PE, *Promenetus exacuous*; VG, *Viviparus georgianus*).

Table 1. Results of a three-way analysis of variance on total abundance of gastropods (TOTDEN), and the abundance of the five most common species. Values are F statistics. There were 44 error degrees of freedom, one degree of freedom for year, four degrees of freedom for sampling group, and two degrees of freedom for depth. (AL, *Amnicola limosa*; GP, *Gyraulus parvus*; HA, *Helisoma anceps*; PG, *Physa gyrina*; VT, *Valvata tricarinata*; *, $P < 0.05$; **, $P < 0.01$).

EFFECT	TOTDEN	AL	VT	GP	PG	HA
Year	4.5*	9.2**	0.2	0.4	.01	1.4
Sampling Group	6.4**	6.0**	6.7**	0.1	0.4	2.2
Yr x Group	1.7	0.2	0.8	0.7	2.1	0.6
Depth	8.1**	9.0**	2.7	0.2	4.0*	4.9*
Yr x Depth	0.6	0.3	0.4	1.9	0.7	0.2
Group x Depth	3.0*	3.1*	2.8*	0.9	0.4	1.0
3-way Interaction	0.5	0.7	0.4	0.8	0.8	0.5

There were complicated changes in the total abundance of gastropods across years, sampling groups and depths (Table 1; Fig. 3). The significant year-effect in the analysis of variance was because of a decrease in gastropod abundance over all sampling groups and depths in 1991. The significant sampling-group effect was because of an increase in abundance of most species later in the field season in both years. There was also a significant trend toward increased gastropod density and diversity in deeper strata. For example, the mean number of species per sample, over both years, was 4.3 for the shallow substratum, 6.3 at intermediate depths, and 6.4 at the deepest depths. Finally, there was a significant interaction between sampling group and depth for total gastropod density. The basic trend appears to be a greater rate of increase in numbers in the shallower depths with time in each season.

The pattern of significance of the F-values in the analysis of variance for *Amnicola limosa*, the most abundant species, was the same as for total gastropod density. This probably indicates that changes in the dynamics of this species are driving the overall effects (Table 1; Fig. 4). Again, densities decreased in 1991 (mean density was lower in 13 of the 15 sampling group and depth combina-

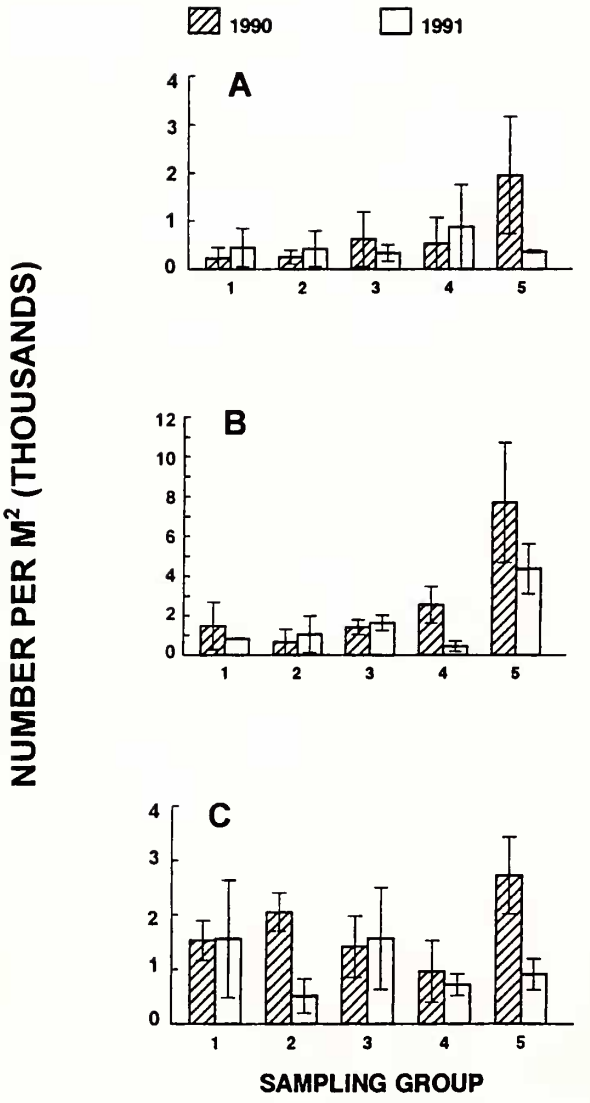

Fig. 3. Total abundance of all gastropod species ± standard errors in five sampling groups in two years, for (A) shallow, (B) intermediate, (C) deep depth strata.

tions [Fig. 4], with a mean reduction in density of 60%). There was also a trend within both years for increased abundances later in the season, with density (averaged over both years and all depth strata) increasing from 473/m² in the first sampling group to 1,765/m² in the last sampling group.

There was also a significant change in abundance with depth for *Amnicola limosa* (over both years and all sampling groups); densities increased from 388/m² in the shallow stratum to a maximum of 1,360/m² at intermediate depths, and dropped to 728/m² in the deep substratum. Finally, there was a greater increase in abundance through time in the shallow and intermediate areas, while densities were more stable in the deep stratum, explaining the significant sampling group by time interaction (Table 1). For example, densities, averaged over both years, increased from 170 /m² in the first sampling group to 622/m² in the last in the shallow stratum, and from 523 to 3,748/m² in the intermediate stratum, but were quite constant in the deep stratum (starting density of 928/m² and ending density of 924/m²).

For *Valvata tricarinata*, only the sampling-group main effect and the sampling group x depth interaction were significant. Averaged over both years and all depth

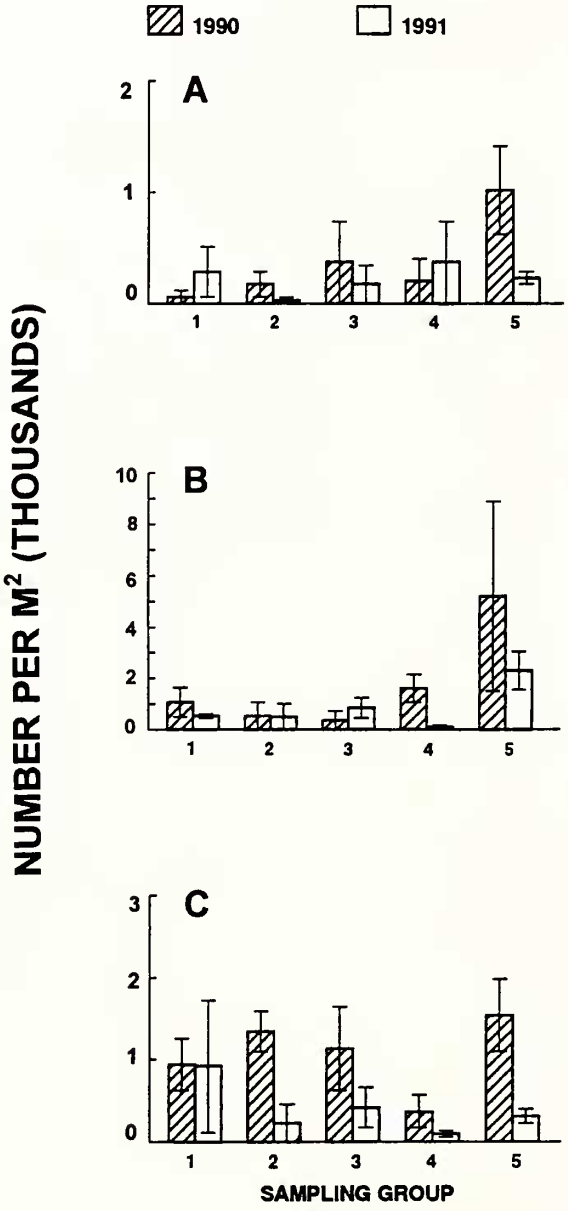

Fig. 4. Abundance of *Amnicola limosa* ± standard errors in five sampling groups in two years, for (A) shallow, (B) intermediate, (C) deep depth strata.

substrata, densities increased from 96/m² in the first sampling group to 661/m² in the fifth sampling group. The significant sampling group x depth interaction probably occurred because densities increased (averaged over both years) from 0 to 354/m² in the shallow stratum from the first to last sampling group, and from 85 to 1,347/m² at intermediate depths. However, they were again fairly constant in the deepest stratum, changing from only 207 to 283/m².

For the remaining three species that had fairly high densities overall (*Gyraulus parvus*, *Physa gyrina*, and *Helisoma anceps*), there were no differences in density between years, or across sampling groups (Table 1). However, there was a significant depth effect for the latter two species. For *P. gyrina*, densities (averaged over all dates and both years) increased from 37 to 207/m². For *H. anceps*, densities actually peaked (127/m²) at the intermediate depth compared to the shallow (22/m²) and deep habitats (48/m²).

At the level of the individual sample, there were significant positive correlations in the abundance of species (Table 2). The abundance of the most common species, *Amnicola limosa*, was positively correlated with each of the four other fairly common species. The abundance of *Valvata tricarinata* was positively correlated with *Physa gyrina* and *Helisoma anceps*. None of the other correlation coefficients were significant. Thus, on a per sample basis, "hot spots" for snail abundance existed, and many species co-occurred at these sites.

MACROPHYTE COLONIZATION EXPERIMENT

The results of this experiment clearly indicate that all four species of gastropod have the same rank-order of macrophyte preference (Fig. 5). The plant main effect was highly significant ($F_{3,79} = 43.8$, $P < 0.0001$), and the plant-snail interaction was not significant ($F_{9,79} = 2.0$, $P = 0.07$), indicating the preference rank was similar in each of the snail species. However, the snail main effect was also highly significant ($F_{3,12} = 13.2$, $P = 0.0004$), indicating differences in colonization rates among snails. *Ceratophyllum demersum* had the lowest colonization rates, averaging 1.6 snails per plant (over all snail species). Next came *Elodea canadensis* with 3.5 snails per plant, *Potamogeton robinsii* with 8.0 snails per plant, and finally *Potamogeton richardsonii* with 12.6 snails per plant. Most gastropods had fairly similar colonization rates, except *Lymnaea emarginata* which had the lowest colonization rates on each macrophyte. This is not surprising, because this species is common on periphyton-covered cobble in shallow water in Wisconsin lakes, not on macrophytes (Weber and Lodge, 1990; Brown and Lodge, 1993). In summary, most gastropods had fairly similar colonization rates on each of the macrophytes tested, and colonized broad-leaved *Potamogeton* species more readily than thinner-leaved species like *Elodea* or *Ceratophyllum*.

Table 2. Pearson product-moment correlations among the abundances of the five most common gastropods in the samples. See Table 1 for species acronyms and symbols for significance.

	AL	VT	GP	PG	HA
AL	1	0.65**	0.25*	0.37**	0.51**
VT		1	-0.02	0.29*	0.37**
GP			1	0.17	0.09
PG				1	0.19
HA					1

DISCUSSION

SPATIAL OVERLAP

The gastropod assemblage of Carrol Lake was quite diverse, with 13 species total, 5-6 of which had fairly high abundances. This is a fairly representative sample of the species present on macrophytes in northern Wisconsin lakes, and is certainly not an exceptionally diverse assem-

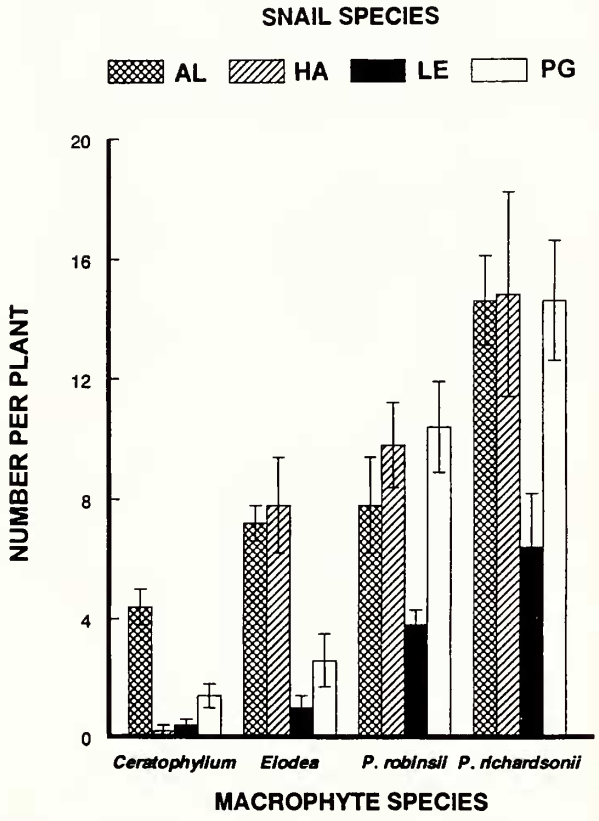

Fig. 5. Mean numbers of four gastropod species colonizing four macrophyte species, ± standard errors. (LE, *Lymnaea emarginata*; see Table 1 for other acronyms).

blage for the area (Brown and Lodge, 1993). The gastropod assemblage was dominated by small, thick-shelled species like *Amnicola* and *Valvata*. Larger species with thick shells, like *Helisoma* spp., *Viviparus georgianus*, and *Campeloma decisum* were present, but rare. The only relatively thin-shelled species (Stein *et al.*, 1984) that attained higher abundances were *Gyraulus parvus* and *Physa gyrina*. The higher relative abundances of small, thick-shelled species could be the result of selective predation by fish, which tend to remove larger, thinner-shelled gastropods (Stein *et al.*, 1984; Osenberg and Mittelbach, 1989; Klosiewski, 1991).

The reduced gastropod abundances in the second year are unexplained, but could indicate significant yearly variation in abundances caused by some abiotic factor (harsh winter weather, etc.). I do not believe the reduced abundances were caused by sampling disturbance, because the area sampled per season was only 0.2 % of the 500 m^2. However, seasonal increases in snail densities in late summer are fairly easy to explain. Most of these gastropods have a spring and early-summer recruitment period, resulting in population increases by the end of the summer (Brown, 1991). The increased densities with depth were probably the result of increased macrophyte biomass at the intermediate and deep strata, because macrophyte density is positively correlated with gastropod density and diversity (Brown and Lodge, 1993). The constancy of numbers through time in the deeper areas, and the increases in shallow areas as the season progressed could be caused by annual migrations. Cheatum (1934) was the first to document movements of snails to deeper water in winter, and back to shallower water in spring, and several others have noticed the same trend (Clampitt, 1974; Boag, 1981). However, an alternative hypothesis would be that snail populations in shallower areas reproduce earlier and thus grow more rapidly because of higher water temperatures (Brown, 1991).

Amnicola limosa was the most abundant species, and it is therefore not surprising that the same treatment effects were significant for this species and gastropod abundance as a whole. Again, densities built up into the field season, were lower in the second year, and increased more with time in shallow areas. For the species in the second tier of abundance, fewer treatment effects could be detected. This could simply be because of their lower abundances and thus patchy distributions (Brown, 1991). The trend for increased abundance with depth, however, occurred for most of the abundant species, again indicating the importance of macrophyte cover to snail abundance.

OVERLAP ON MACROPHYTES

At the level of the individual sample, the most common species had positive correlations among themselves in abundance. This is probably because of the patchy distribution of snails in general: certain sites had higher snail densities of all species, probably because of variation in macrophyte diversity and cover, etc., among samples. For example, certain species of macrophytes might have greater periphyton abundances or periphyton species of higher nutrient quality, differ in their accessibility to snail grazers, or offer more of a refuge from predation. All of these hypotheses deserve further study. These data do indicate, however, that there is little spatial partitioning at the scale of the microhabitat among these snail species.

In fact, the laboratory experiment suggests that there is almost a remarkable degree of similarity in colonization rates of a group of macrophytes among the four species of snails studied. The snails all prefer broader-leaved species like *Potamogeton* over thin-leaved species like *Elodea* or *Ceratophyllum*. Several mechanisms could produce such results. Either broader-leaved species are colonized by a richer periphyton assemblage, or broader-leaved species could have growth forms more suitable for colonization, or broader-leaved species could provide more of a refuge from visually orienting predators. The first and last hypotheses remain unexplored, but the second hypothesis contradicts a laboratory study by Kershner and Lodge (1990). Kershner and Lodge found higher colonization rates by two snail species on more finely divided artificial macrophytes (*e. g.* that would mimic thinner-leaved species like *Elodea* or *Ceratophyllum*), but did conclude that the particular relationship of macrophyte growth form to colonization rate depended on the animal group under study. Whatever the underlaying mechanism, the data suggest there is little potential for differential use of macrophytes to be a mechanism of niche partitioning by snail species. In fact, the similar patterns of macrophyte choice among species could explain why there were positive correlations among the abundances of the most common species in the sampling data.

ACKNOWLEDGMENTS

I would like to thank Yvonne Vadeboncoeur and various workers for help in collecting benthic gastropod samples, and Edward Haight for help with the macrophyte choice experiments. Drs. Roy Stein and David Lodge gave helpful advice on sampling and experimental design. The work was funded by NSF grant 89-07690.

LITERATURE CITED

Boag, D. A. 1981. Differential depth distribution among freshwater snails subjected to cold temperatures. *Canadian Journal of Zoology* 59:733-737.

Brown, C.L., T. P. Poe, J. R. P. French, and D. W. Schoesser. 1988. Relationships of phytomacrofauna to surface area in naturally occurring macrophyte stands. *Journal of the North American Benthological Society* 7:129-139.

Brown, K. M. 1982. Resource overlap and competition in pond snails: an experimental analysis. *Ecology* 63:412-422.

Brown, K. M. 1991. Mollusca: Gastropoda. *In: Ecology and Classification of North American Freshwater Invertebrates,* J. Thorp and A. Covich, eds. pp. 285-314. Academic Press, New York.

Brown, K. M. and D. M. Lodge. 1993. Gastropod abundance in vegetated habitats: the importance of specifying null models. *Limnology and Oceanography* 38:217-225.

Cheatum, E. P. 1934. Limnological investigations on respiration, annual migratory cycle, and other related phenomena in freshwater pulmonate snails. *Transactions of the American Microscopical Society* 53:348-407.

Clampitt, P. T. 1974. Seasonal migration cycle and related movements of the freshwater pulmonate snail, *Physa integra. American Midland Naturalist* 92:275-300.

Kershner, M. W. and D. M. Lodge. 1990. Effect of substrate architecture on aquatic gastropod-substrate associations. *Journal of the North American Benthological Society* 9:319-326.

Klosiewski, S. P. 1991. *The Role of Pumpkinseed Sunfish in Structuring Snail Assemblages in Northern Wisconsin Lakes.* Doctoral Dissertation, Ohio State University, Columbus, Ohio. 147 pp.

Lodge, D. M., K. M. Brown, S. P. Klosiewski, R. A. Stein, A. P. Covich, B. K. Leathers, and C. Bronmark. 1987. Distribution of freshwater snails: spatial scale and the relative importance of physicochemical and biotic factors. *American Malacological Bulletin* 5:73-84.

Lodge, D. M., M. W. Kershner, J. P. Aloi, and A. P. Covich. 1994. Effects of an omnivorous crayfish *(Orconectes rusticus)* on a freshwater littoral food web. *Ecology* 75:1265-1281.

Osenberg, C. W. and G. C. Mittelbach. 1989. Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. *Ecological Monographs* 59:405-432.

Stein, R. A., C. G. Goodman, and E. A. Marschall. 1984. Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology* 65:702-715.

Weber, L. M. and D. M. Lodge. 1990. Periphytic food and predatory crayfish: relative roles in determining snail distribution. *Oecologia* 82:33-39.

Date of manuscript acceptance: 04 September 1997